10
Role in Ecosystem and Global Processes

10A. Decomposition

1. Introduction

Decomposition of plant litter involves the physical and chemical processes that reduce litter to CO_2, water, and mineral nutrients. It is a key process in the **nutrient cycle** of most terrestrial ecosystems, and the amount of carbon returned to the atmosphere by decomposition of dead organic matter is an important component of the global carbon budget (Sect. 2.6 of Chapter 10B on ecosystem and global processes; Chapin et al. 2002).

Sooner or later, plant material that has not been consumed by herbivores or pathogens, or lost through a fire, is decomposed. Only a small proportion of recalcitrant organic matter and products of microbial decomposition become stabilized for thousands of years as **humus**. Most root-released material (exudates and other root-derived organic matter) is incorporated in the soil microbial biomass or lost as CO_2 within weeks, at least at a high nutrient supply. When nutrients limit growth, soil microorganisms utilize the root-derived material more slowly because microbial growth is limited by nutrients, rather than by carbon (Schimel & Bennett 2004). In wet, anoxic environments, some of it may end up as peat, or even coal. In that case, carbon is temporarily removed from the global carbon cycle. The rate of **carbon sequestration** in peatlandsis mainly determined by low rates of decomposition of dead organic matter, rather than high rates of primary production. Due to the relatively large peat cover on Earth, changes in the extent to which peatlands act as a CO_2-sink will affect the global carbon budget (Gorham 1991).

N and P are released enzymatically during decomposition. Proteins and other N-containing polymers are broken down to monomers (amino acids, nucleotides) that can be absorbed by plants or soil microorganisms (Chapin et al. 2002). Under low-N conditions, plants and microorganisms (including mycorrhizal fungi) compete for this organic N. As N availability increases, this competition becomes less intense, and soil microorganisms become more energy limited. Under these circumstances, they break down amino acids to meet their energy demands and convert N to inorganic forms (NH_4^+ and NO_3^-), which are excreted and can be absorbed by other microbes or plants (**N mineralization**) (Schimel and Bennett 2004). **P mineralization** differs from that of N in that P_i is cleaved from P-containing polymers by plant or microbial phosphatases without breakdown of the associated carbon skeleton (Sect. 2.1.2 of Chapter 6 on mineral nutrition). P and C mineralization and the formation of N-containing monomers occur external to microbial cells, whereas N mineralization occurs within microbial cells.

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2. Litter Quality and Decomposition Rate

2.1 Species Effects on Litter Quality: Links with Ecological Strategy

In a comparison of 125 British vascular plant species, which cover a wide range of life forms, leaf habits, and taxa, the rate of leaf litter decomposition can be predicted from a limited number of whole-plant traits, reflecting the plants' physiological and structural adaptation to environment (Fig. 1; Cornelissen 1996, Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000). These traits include life-form, deciduous vs. evergreen habit, leaf toughness, autumn coloration of the leaf litter, family and a species' success in disturbed and productive habitats. In this wide comparison of species from the British Isles, as in other comparisons (Aerts 1997), there is a negative relationship between decomposition rate and **leaf life span**. For example, leaves of woody climbers and ramblers, which tend to have short-lived leaves with little investment in quantitatively important defense compounds, decompose more readily than those of subshrubs, which often inhabit infertile habitats and invest more in chemicals that reduce leaf digestibility and palatability, such as lignin and tannins (Sect. 3.2 of Chapter 9B on ecological biochemistry).

Across species and plant functional types, the **specific leaf area** (SLA) tends to be positively correlated with the rate of decomposition of the leaf litter (Cornelissen et al. 1999, Garnier et al. 2004). Long-lived leaves, with relatively large investments in quantitatively important chemical defense, tend to have a lower SLA (Wright et al. 2005). This accounts for the positive correlation between rate of litter decomposition and SLA. Deviations from this relationship may be due to variation in other leaf traits that do not influence SLA much, but do have afterlife effects on litter decomposition. Such traits include, for instance, cuticle structure, mobile secondary (defense) chemistry, and tissue pH (Swift et al. 1979, Cornelissen et al. 2006). The association between autumn colors and decomposition is also a reflection of the leaf's secondary chemistry (Fig. 1). Brown colors are associated with phenolics, which slow down the rate of decomposition, in a manner similar to their effects on protein digestion (Sect. 3.2 of Chapter 9B on ecological biochemistry).

Litter turnover is also closely associated with mycorrhizal type. Species with **ericoid mycorrhizas** typically have poor litter decomposability, compared with **ectomycorrhizal species**, whereas **arbuscular mycorrhizal** plant shows comparatively fast litter decomposition. These results indicate that within a representative subset of a flora, ericoid and ectomycorrhizal strategies are linked with low ecosystem turnover and arbuscular mycorrhizal species with high ecosystem turnover (Cornelissen et al. 2001).

To explain the biochemical basis of variation in leaf litter decomposition, more information is required about **leaf chemistry**: rates of litter decomposition are negatively correlated with both the

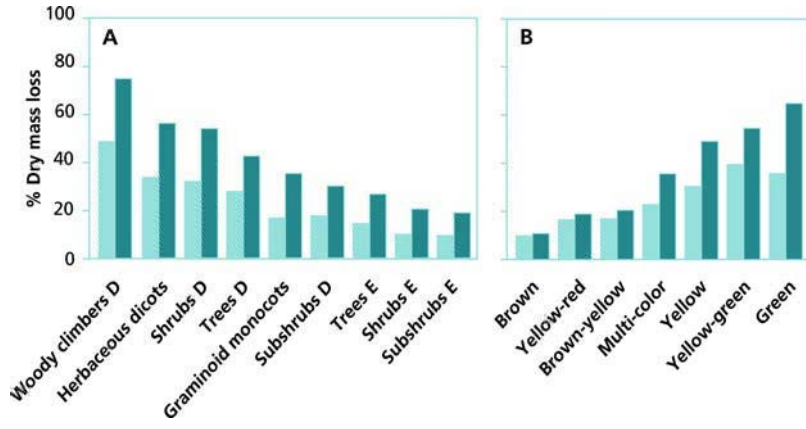

FIGURE 1. Mass loss (% of original mass) of litter of 125 British species as related to (A) growth form and duration of decomposition period (8 weeks, *closed bars*; 20 weeks, *open bars*) or (B) initial litter color (for deciduous woody species only) and mesh size of the bag that contained the litter (0.3 mm mesh, *closed bars*; 5 mm mesh, *open bars*). D = deciduous; E = evergreen. Litter was buried in leaf mould near Sheffield, England. Means were calculated from mean values of individual species (based on information in Cornelissen 1996).

lignin:nutrient ratio (N or P) and the **lignin concentration** (Berg & Staaf 1981, Berendse et al. 1989, Fox et al. 1990). **Polyphenols** also affect litter quality, and may in some cases have a larger effect than N or lignin (Hättenschwiler & Vitousek 2000). For example, *Sphagnum* (peat moss) species produce **phenolic compounds**, the most important one being sphagnum acid. Decomposition of *Sphagnum* litter is remarkably slow because of the anoxic, acidic conditions in the bog environment (Sect. 2.2) and also because of the chemical composition of the acidic litter (Johnson & Damman 1993, Cornelissen et al. 2006). Leachates from *Sphagnum* species reduce the decomposition rate of litter from other plants as well (Verhoeven & Toth 1995). Decomposition rate often correlates inversely with C:N ratio, especially among herbaceous species, which vary in N and P concentrations, but typically have low concentrations of quantitative defensive compounds in leaves. Thus both carbon and nutrient chemistry influence decomposition rate, although their relative importance may vary across species.

Species differences in allocation strongly influence decomposition because of the strikingly different chemistry of leaves, wood, and roots. Stems and roots, with their high lignin and low N concentration, decompose more slowly than do leaves. Species differences in litter quality due to differences in allocating wood vs. leaves often exceed differences due to the variation in leaf quality (Hobbie 1995). For example, dwarf birch (*Betula nana*), a tundra deciduous shrub, has a low overall decomposition rate, when all plant parts are included, despite relatively rapid rates of leaf decomposition (Fig. 2). Woody stems of slow-growing, late-successional species, with their higher concentrations of quantitative defenses, tend to decompose more slowly than do less dense woody stems of rapidly growing species (Chambers et al. 2000, Eaton & Lawrence 2006).

We know relatively little about species differences in **root decomposition**, despite the large proportion of litter production that occurs below ground. Fine roots generally decompose in weeks to months, whereas coarse roots are much slower to decompose (Ruess et al. 1996). Variation in root decomposition among species or functional types is associated more with variation in root litter quality, and less so with climate-linked variables (Silver & Miya 2001).

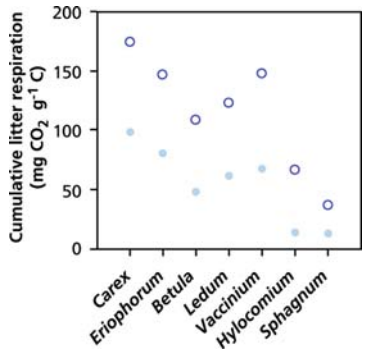

FIGURE 2. Cumulative respiration of litter of seven Alaskan tundra species incubated in the laboratory with tundra soil over 149 days at either 4°C (*filled circles*) or 8°C (*open circles*). Each litter bag has the same initial mass but includes leaves, stems, and roots in proportion to their production in the field. Litter respiration is estimated by subtracting the average respiration in the controls (soil only) from the total respiration in those incubations amended with litter (Hobbie 1996). Copyright by the Ecological Society of America. Species include from left to right: two sedges, three dwarf shrubs, and two mosses.

2.2 Environmental Effects on Decomposition

Environment affects decomposition both because of its effect on the quality of litter produced and because of its direct effects on microbial activity (Swift et al. 1979). The direct effects of environment on microbial activity are similar to effects on plant production, resulting in highest rates of decomposition in warm, moist environments (Sect. 2.5 of Chapter 10B on ecosystem and global processes). In anaerobic soils (e.g., in peatlands), decomposition is more restricted than is plant production, which results in substantial **carbon sequestration** (Sect. 1). Plant species strongly influence decomposition through their effect on environment. For example, arctic mosses are effective thermal insulators, resulting in cold soils that retard decomposition even more than might be expected from their low litter quality (Hobbie 1995).

Microbial respiration associated with the decomposition of surface litter is often enhanced at night because dew provides moisture for microbial activity and decreases during the day as the litter dries out (Edwards & Sollins 1973). In dry environments, the moister conditions beneath vegetation may favor decomposition. In particularly sunny and dry environments, **photodegradation** can be an important process for litter breakdown, even dominating over microbial decay (Austin & Vivanco 2006).

Environment also affects tissue chemistry, and therefore litter quality. The higher tissue N and P concentrations in plants on fertile soils result in high litter nutrient concentrations (Table 21 in Chapter 6 on mineral nutrition) and therefore high rates of decomposition. Among woody plants, growth in infertile soils also increases **quantitative defenses**, further contributing to the slow decomposition of litter produced on these soils (Sect. 4.1 of Chapter 9B on ecological biochemistry). Reciprocal transplants of litter among forests, which differ strongly in litter quality and environment, often show that litter quality exerts a stronger effect on decomposition than do differences in temperature or moisture (Flanagan & Van Cleve 1983).

3. The Link Between Decomposition Rate and Nutrient Supply

3.1 The Process of Nutrient Release

A major reason for interest in decomposition is its close link to **nutrient supply**. In most ecosystems, the nutrients released during decomposition provide >90% of the N and P supply to plants (Table 21 in Chapter 6 on mineral nutrition). Our understanding of the processes by which nutrients are released from plant litter and become available to plants has improved considerably in recent years. In a comparison of herbaceous species in Britain, the best predictor of the rate of leaf litter decomposition is total concentration of Ca, Mg, and K in green leaves (Cornelissen & Thompson 1997). The relatively high litter pH associated with a high Ca concentration may favor microbial decomposition (Cornelissen et al. 2006). Interspecific variation in pH and base content of leaf litter may partly explain why the correlations of litter decomposition with C:N are often much poorer than predicted by theory.

P is ester bonded to carbon skeletons in plant litter. However, its release is only indirectly linked to decomposition because the ester bond is readily cleaved by **phosphatases** without breakdown of the associated carbon skeleton. Phosphatases are produced by plant roots, ectomycorrhizal and ericoid **mycorrhizal fungi**, and **saprophytic microorganisms** (i.e., those microorganisms whose energy supply is derived from dead organic matter). Decomposition is indirectly linked to P release because decomposition rate determines microbial demand for P and therefore the rate of production of microbial phosphatases. In addition, decomposition of cell walls by fungi increases access of microbial phosphatases to P-containing compounds in plant litter.

N is the nutrient whose release from plant litter is most tightly linked to decomposition because, like decomposition, it requires the breakdown of organic compounds in plant litter. In many biomes, the first steps in decomposition are consumption by invertebrate fauna that reduce the size of litter particles. This step is important for **cuticle** damage, allowing access of microbes to the tissues and leaching of mobile phenols once membranes are ruptured (Swift et al. 1979). Subsequent N release involves the breakdown of **particulate organic N** (PON; polymers such as proteins and nucleic acids) to **dissolved organic N** (DON), i.e., compounds that are small enough (e.g., amino acids and nucleotides) to be absorbed by microbial cells (Fig. 3). DON production is catalyzed by microbial **exoenzymes** (enzymes that are secreted by microbial cells into

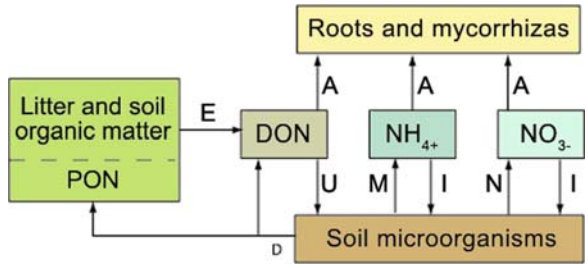

FIGURE 3. Simplified diagram of microbially mediated N transformations in soils. Particulate organic nitrogen (PON) in plant litter and soil organic matter is broken down to dissolved organic N (DON) by exoenzymes (E); this is the rate-determining process in supplying plant-available N. Soil microorganisms take up (U) DON and use it to support their growth if they are N-limited; they also immobilize (I) NH_4^+ and NO_3^-, if present. If microorganisms are energy limited, they break down DON for energy, and excrete NH_4^+, the process of N mineralization (M), or NO_3^-, the process of nitrification (N). Plants and their mycorrhizas absorb (A) some combination of DON, NH_4^+, and NO_3^-, depending on relative availability.

the soil matrix) and is typically the rate-limiting step in N release from plant litter (Chapin et al. 2002). Both mycorrhizas (especially ectomycorrhizas) and saprophytes produce exoenzymes that convert PON to DON. DON can then be absorbed by saprophytes, plant roots, and their mycorrhizal partners. Under strongly N-limiting conditions (e.g., tundra and peatlands), microbial growth is extremely N-limited, so all DON absorbed by microorganisms supports microbial growth, and negligible N mineralization occurs; under these circumstances, DON is the predominant form of N absorbed by all soil organisms, including plants (Schimel and Bennett 2004). In less N-limited environments (e.g., conifer forests), some N mineralization occurs in N-rich microsites, where microbes are energy limited and use DON as an energy source, excreting NH_4^+ as a waste product (**N mineralization**), which diffuses into the bulk soil from these N-rich microsites. In these environments, plants and other microorganisms absorb both DON and NH_4^+ to meet their N demands. In extremely fertile soils, most soil microsites are N-rich, so breakdown of DON to NH_4^+ occurs abundantly and meets microbial energy demands. Some of this NH_4^+ is absorbed by nitrifying bacteria that use NH_4^+ as an energy source and excrete NO_3^- as a waste product (**nitrification**). In summary, across a soil fertility gradient (which often correlates with a gradient in soil pH), the relative availability of N utilized by plants ranges from predominantly DON in infertile, often acidic soils to NH_4^+ in soils of intermediate fertility, to predominantly NO_3^- in fertile soils.

Sulfur (S) is intermediate between N and P in terms of its linkage to decomposition because some S is ester bonded (like P) and can be released by **sulfatases** without decomposition, but other S atoms are covalently linked and require decomposition to dissolved organic forms before they can be absorbed and metabolized by soil microorganisms (Mitchell & Fuller 1988).

3.2 Effects of Litter Quality on Mineralization

When litter or soil organic matter contains nutrients in excess of microbial demands, N and P are excreted by soil microorganisms (net **mineralization**) during the decomposition process and become available for plant uptake (Sect. 3.1, Fig. 6.2 in Chapter 6 on mineral nutrition). On the other hand, if the organic matter is low in nutrients, microorganisms meet their nutrient demand by absorbing nutrients from the soil solution (net **immobilization**), resulting in competition for nutrients between soil microorganisms and plants. After nutrient resorption (Sect. 4.3.2 of Chapter 6 on mineral nutrition), plant litter often has a higher C:N ratio than microbial biomass. Empirical observations suggest that above a critical C:N ratio of about 20:1, microorganisms absorb nutrients from the soil solution, causing net N immobilization (Paul & Clark 1989). As microorganisms decompose the organic matter and respire carbon to meet respiratory demands for growth and maintenance, the C:N ratio of litter declines. Net N mineralization occurs when the C:N ratio falls below the critical 20:1 ratio. The result is that fresh litter often initially increases in N concentration due to microbial immobilization, before net mineralization occurs. In many P-limited forest ecosystems, P is immobilized to a significantly greater extent than is N in the first stages of decomposition (Attiwell & Adams 1993).

Net immobilization occurs to a greater extent and for a longer time where plants produce litter with low tissue N and P concentrations. In those ecosystems where plant growth is N-limited, litter C:N ratios strongly govern decomposition and N immobilization, with P being mineralized more quickly, whereas in areas of heavy **N deposition**, as in the Netherlands, C:P ratios exert stronger control over decomposition, and N is mineralized more quickly (Aerts & De Caluwe 1997). The high litter N and P concentrations of plants on fertile soils, with their high growth rate and SLA, thus promote nutrient mineralization, whereas there is slower mineralization in ecosystems dominated by slow-growing plants with low SLA (Hobbie 1992, Van Breemen 1993).

If nutrient concentration affects mineralization so strongly, then will the low tissue nutrient concentrations caused by **elevated atmospheric CO_2 concentrations** reduce litter nutrient concentrations and therefore decomposition rate? In most cases studied to date, differences in leaf chemistry caused by elevated [CO_2] diminish during senescence, perhaps due to respiration of accumulated starch, so that litter quality and therefore decomposition and mineralization rates are similar for litter produced under elevated and ambient [CO_2] (Norby et al. 2001). Elevated atmospheric CO_2 concentrations only cause accumulation of soil carbon when N is added at rates well above typical atmospheric N inputs. Soil carbon sequestration under elevated CO_2 is constrained both directly by N availability and indirectly by nutrients needed to support N_2 fixation (Sect. 3.8 in Chapter 9A on symbiotic associations; Van Groenigen et al. 2006).

Species differences in the types of carbon compounds they contain magnify differences in mineralization rate due to litter nutrient concentration. The high concentrations of quantitative secondary metabolites in species with long-lived leaves (Sect. 2.1) retard decomposition because of both the toxic effects on microorganisms and the difficulty of breakdown of secondary metabolites. **Phenolic** compounds that are decomposed slowly include lignin and tannin (Sect. 3.2 of Chapter 9B on ecological biochemistry). High tannin concentrations reduce the rate of **mineralization** of the litter, so that, for instance, most of the N in the boreal forest soil occurs as complexes of organic N and tannin, rather than as NO_3^-, NH_4^+, or amino acids (Northup et al. 1995). Tannins and other protein-binding phenolics also inhibit **nitrification**, the microbial conversion of ammonia, via NO_2^- to NO_3^- (Baldwin et al. 1983). In many species, including *Pinus* (pine), the concentration of tannin and lignin is enhanced when plants are grown under N limitation as compared with an optimum N supply (Bryant et al. 1983, Gershenzon 1984). As a result, the availability of N is even further reduced, at least for plants lacking mechanisms to release N from the tannin–organic N complexes (Sect. of Chapter 9A on symbiotic associations; Northup et al. 1995, Aerts & De Caluwe 1997).

There is clear evidence that some **mycorrhizal fungi** produce enzymes that allow them to derive mineral nutrients and carbon from organic sources (Sect. 2.4 of Chapter 9A on symbiotic associations). Especially, **ectomycorrhizas** and **ericoid mycorrhizas** are capable of using relatively complex organic N sources (Sect. 2.4 of Chapter 9A on symbiotic associations), possibly including the complexes produced under pine stands growing under nutrient-poor conditions. A direct release of N from organic compounds by ectomycorrhizal fungi seems to be confined to the older litter layers (Colpaert & Tichelen 1996).

For nonmycorrhizal species in nutrient-poor environments, associations with mycorrhizal fungi cannot provide access to complexes of organic N with tannins. In nonmycorrhizal *Rhizophora mangle* (red mangrove), defenses are largely carbon-based (**quantitative**; Sect. 3.3 of Chapter 9B on ecological biochemistry). These plants have long been used for their high proanthocyanidin (condensed tannin) content of their wood, bark, and leaves. **Polyphenolics** account for approximately 23% of the total leaf dry mass. Interestingly, during leaf senescence, prior to leaf abscission, polyphenols largely disappear, leaving only the largest tannin polymers. The ecological significance of these changes may be that litter decomposition in the mangrove swamps would be greatly inhibited by the phenolic compounds that are broken down before leaf abscission. This breakdown would favor litter decomposition, rather than render the litter poorly available as is the case for pine needles. Since mycorrhizal associations are not a strategy available mangrove swamps, breakdown of phenolic compounds before leaf abscission may be an alternative strategy to the one discussed above for mycorrhizal pines (Kandil et al. 2004). Indeed, leaf litter of *Rhizophora mangle* decomposes within 5 months (Middleton & McKee 2001).

In situations where the N availability is low because of plants that produce phenolics, invasion of grasses [*Molinia caerulea* (cotton grass) and *Deschampsia flexuosa* (tufted hair-grass)] into nutrient-poor habitats dominated by ericaceous dwarf shrubs [*Calluna vulgaris* (Scottish heather) and *Erica tetralix* (crossleaf heath)] may enhance rates of **mineralization**. Such invasions are made possible by N deposition, due to **acid rain**. They may enhance the rate of N cycling in the system because organic N contained in the litter of the grasses is mineralized faster than that in residues of the dwarf shrubs (Van Vuuren et al. 1992). Similarly, increased fire frequency in nutrient-poor Mediterranean woodlands may enhance P availability and weed invasion, which then further enhances the rate of nutrient cycling (Fisher et al. 2006).

3.3 Root Exudation and Rhizosphere Effects

The presence of living roots can greatly enhance litter decomposition and mineralization, either by directly using organic matter in the litter through associations with ectomycorrhizal fungi (Sect. 4.2 of Chapter 9A on symbiotic associations) or by providing a carbon source that either stimulates or retards the growth and activity of soil microorganisms and nematodes (Cheng & Coleman 1990, Griffiths et al. 1992, Zhu & Ehrenfeld 1996). There may be either positive or negative effects of roots on mineralization, depending on environmental conditions.

Root exudates are released in response to a limiting supply of P or micronutrients or to toxic levels of some metals (Sects. 2.25, 2.2.6, 3.1.3, and 3.3.4 of Chapter 6 on mineral nutrition; Farrar et al. 2003, Nguyen 2003). They stimulate mineralization only if microorganisms consume the exuded carbohydrates and, in addition, decompose soil organic matter in the rhizosphere or are grazed by soil animals. Gram-negative bacteria with high growth rates, but a low capability to degrade complex substrates, are

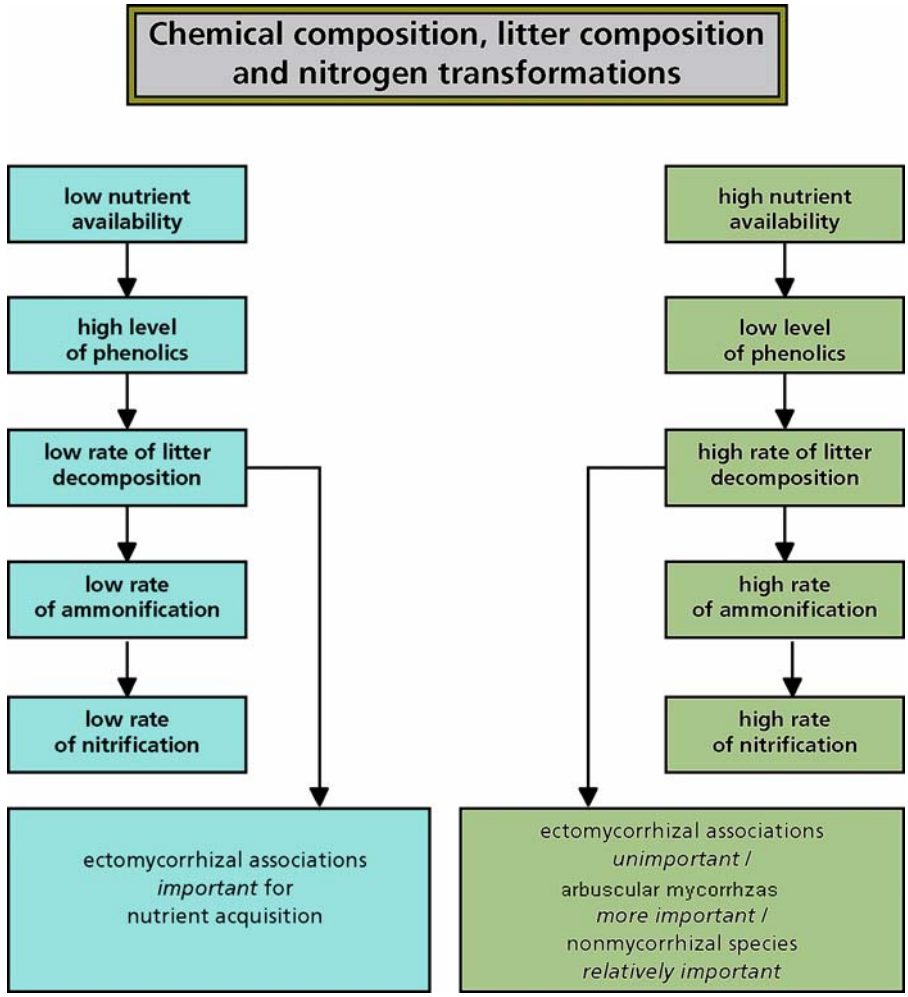

FIGURE 4. Generalized scheme to account for effects of chemical composition of biomass and litter on rates of decomposition and nitrification (see also Read & Perez-Moreno 1993). Only two extreme situations are shown, with many intermediate habitats or stages of succession occurring between these extremes. Rates of litter decomposition as dependent on nutrient supply in the habitat. In slow-growing species growing in low-nutrient soils (*left*), the concentrations of N and P tend to be low and phenolics accumulate. These phenolics act as digestibility-reducing defense compounds in the living plant. They also reduce the rate of litter decomposition, thus reducing the rate at which nutrients become available for plant growth. Some mycorrhizal associations, but not AM, may access complexes of organic N and phenolics, and thus make N available for plant growth. Such mycorrhizal associations are absent in nearly all herbaceous species and some woody species, but are common in, e.g., ericaceous and coniferous species. Ectomycorrhizal associations predominate among the woody species. Nonmycorrhizal species (e.g., Proteaceae) dominate when P is poorly available because the total amounts of P are low and predominantly sorbed to soil particles. In plants growing in high-nutrient soils (*right*), the concentration of nutrients is high and that of phenolics is low. The litter of these plants also has low concentrations of phenolics and relatively higher nutrient levels. Consequently, it is readily decomposed, releasing NH_4^+ that is either absorbed by plant roots or used by soil microorganisms. Some of these microorganisms (*Nitrosomonas*) use NH_4^+ as an energy source, oxidizing it to NO_2^-, which is then further oxidized to NO_3^- by other soil microorganisms (*Nitrobacter*). The entire process, from NH_4^+ to NO_3^-, is called nitrification. It occurs more rapidly in the high-nutrient environment of faster-growing plants. Arbuscular mycorrhizas are more common in high-nutrient environment of the faster growing species. Nonmycorrhizal, ruderal species may dominate during the earliest stages of succession, when soil P levels are relatively high and P_i is readily available; nonmycorrhizal species with root clusters dominate at very late stages of succession, when there is little soil P and most P_i is sorbed.

generally the major microorganisms that are stimulated by exudation. For example, when wheat (*Triticum aestivum*) or rye (*Secale cereale*) plants are grown in soil with ^{14}C-labeled straw, only 6% of the microbial biomass is labeled with ^{14}C. This microbial biomass, however, is highly active in releasing $^{14}CO_2$, indicating a "**priming**" of decomposition by the exudates (Cheng & Coleman 1990, Carney et al. 2007). Under conditions of low nutrient availability, this priming effect is often less pronounced, perhaps because bacteria have insufficient nutrients to grow and attack soil organic matter (Van Veen et al. 1989) and because plants may intensely compete with soil microorganisms for nutrients under these conditions (Norton & Firestone 1996). This may explain why agricultural and other mineral soils often show a **positive effect** of roots on N mineralization (Van Veen et al. 1989, Bottner et al. 1991), whereas these effects are less pronounced or **negative** in infertile or highly organic soils (Harris & Riha 1991, Tate et al. 1991, Parmelee et al. 1993). Similarly, roots of tree seedlings stimulate N mineralization in fertile mull soils, but decrease mineralization in infertile highly organic mor soils (Bradley & Fyles 1996). **Root exudates** may be effective in **priming** mineralization of fertile mull soil organic matter because of its relatively labile carbon. By contrast, lignolytic activity may control soil N turnover in infertile mor soils, where bacteria stimulated by root exudates lack the enzymatic capacity to degrade lignin. Thus, soil fertility may determine the nutritional consequences of root exudation both through its effect on the C/N balance of bacteria and through its effects on the recalcitrance of soil organic matter.

Roots may also promote mineralization as a result of more intense grazing of bacteria by protozoa. The increased growth of bacteria in response to exudates in the rhizosphere attracts protozoa, which use the bacterial carbon to support their growth and maintenance; the protozoa excrete the mineralized nutrients, which are then available for uptake by the plant (Clarholm 1985). We expect this nutrient release by bacterial grazers to be most pronounced in fertile soils, where bacterial growth rates would be highest. The rapid bacterial growth in response to root exudates can also positively affect the plant by outcompeting microorganisms that have detrimental effects on plants.

There are obviously major technical difficulties in studying the complex biotic interactions that may occur in the rhizosphere. However, recent molecular advances now enable the discovery of novel microorganisms with unforeseen metabolic capabilities, revealing new insight into the underlying processes regulating nutrient cycles at local to global scales. With the ability to sequence functional genes from the environment, molecular approaches now enable us to identify microorganisms and metabolic processes and develop an understanding of many globally important biogeochemical processes (Zak et al. 2006).

Elevated [CO_2] can influence mineralization through its effects on rhizosphere processes, but CO_2 effects on microbial processes vary, depending on the plant species present and soil fertility (Van Groenigen et al. 2006). Plant species composition influences how soil N cycling will respond to further increases in [CO_2] (Hungate et al. 1996, Carney et al. 2007). The nature of the rhizosphere community affects the quantity and quality of root exudates, with much higher exudation rates occurring in nutrient-poor soils than in common solution culture. Different populations of soil bacteria and fungi can have distinct effects on the quantity and quality of root exudates (Leyval & Berthelin 1993, Rygiewicz & Andersen 1994) and therefore on patterns of mineralization in the rhizosphere.

4. The End Product of Decomposition

Decomposition of plant litter is a key process of the nutrient cycles of most terrestrial ecosystems. Rates of decomposition strongly depend on chemical composition, with slower rates being associated with acidic litter with a low base content, low concentrations of N or P, and high concentrations of phenolics (tannin, lignin). Since plants in nutrient-poor habitats tend to accumulate more quantitative secondary plant compounds and have low base and N and P concentrations, their litter is decomposed rather slowly, thus aggravating the low-nutrient status in these habitats. Some mycorrhizal associations appear pivotal in accessing N in litter containing high concentrations of phenolics (Fig. 4).

References

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos* **79**: 439–449.

Aerts, R. & De Caluwe, H. 1997. Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. *Ecology* **78**: 244–260.

Attiwell, P.M. & Adams, M.A. 1993. Nutrient cycling in forests. *New Phytol.* **124**: 561–582.

Austin, A.T. & Vivanco, L. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* **442**: 555–558

Baldwin, I.T., Olson, R.K., & Reiners, W.A. 1983. Protein-binding phenolics and the inhibition of nitrification in subalpine balsam fir soils. *Soil Biol. Biochem.* **15**: 419–423.

Berendse, F., Bobbink, R., & Rouwenhorst, G. 1989. A comparative study on nutrient cycling in wet heathland ecosystems. II. Litter decomposition and nutrient mineralization. *Oecologia* **78**: 338–348.

Berg, B. & Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. *Ecol. Bull.* **33**: 163–178.

Bottner, P., Cortez, J., & Sallih, Z. 1991. Effect of living roots on carbon and nitrogen of the soil microbial biomass. In: Plant root growth, D. Atkinson (ed.). Blackwell Scientific, London, pp. 201–210.

Bradley, R.L. & Fyles, J.W. 1996. Interactions between tree seedling roots and humus forms in the control of soil C and N cycling. *Biol. Fertil. Soils* **23**: 70–79.

Bryant, J.P., Chapin III, F.S., & Klein, D.R.. 1983. Carbon/nutrient balance of boreal plants in relation to herbivory. *Oikos* **40**: 357–368.

Carney, K.M., Hungate, B.A., Drake, B.G., & Megonigal, J.P. 2007. Altered soil microbial community at elevated CO_2 leads to loss of soil carbon. *Proc. Natl. Acad. Sci. USA* **104**: 4990–4995.

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L.V., & Melack, J.M. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* **122**: 380–388.

Chapin III, F.S., Matson, P.A., & Mooney, H.A. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag, New York.

Cheng, W. & Coleman, D.C. 1990. Effect of living roots on soil organic matter decomposition. *Soil Biol. Biochem.* **22**: 781–787.

Clarholm, M. 1985. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Biochem.* **17**: 181–187.

Colpaert, J.V. & Van Tichelen, K.K. 1996. Decomposition, nitrogen and phosphorus mineralization from beech leaf litter colonized by ectomycorrhizal or litter-decomposing basidiomycetes. *New Phytol.* **134**: 123–132.

Cornelissen, J.H.C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *J. Ecol.* **84**: 573–582.

Cornelissen, J.H.C. & Thompson, K. 1997. Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytol.* **135**: 109–114.

Cornelissen, J.H.C., Perez-Harguindeguy, N., Diaz, S., Grime, J.P., Marzana, B., Cabido, M., Vendramini, F., Cerabolini, B. 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytol.* **143**: 191–200.

Cornelissen, J.H.C., Aerts, R., Cerabolini, B., Werger, M.J.A., & Van der Heijden, M.G.A. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia.* **129**: 611–619.

Cornelissen, J.H.C., Quested, H.M., van Logtestijn, R.S.P., Pérez-Harguindeguy, N., Gwynn-Jones, D., Díaz, S., Callaghan, T.V., Press M.C., & Aerts, R. 2006. Foliar pH as a new plant trait: Can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia* **147**: 315–326.

Edwards, N.T. & Sollins, P. 1973. Continuous measurement of carbon dioxide evolution from partitioned forest floor components. *Ecology* **54**: 406–412.

Eaton, J.M. & Lawrence, D. 2006. Woody debris stocks and fluxes during succession in a dry tropical forest. *For. Ecol. Manage.* **232**: 46–55.

Farrar, J., Hawes, M., Jones, D. & Lindow, S. 2003. How roots control the flux of carbon to the rhizosphere. *Ecology* **84**: 827–833.

Fisher, J.L., Veneklaas, E.J., Lambers, H., & Loneragan, W.A. 2006. Enhanced soil and leaf nutrient status of a Western Australian *Banksia* woodland community invaded by *Ehrharta calycina* and *Pelargonium capitatum*. *Plant Soil* **284**: 253–264.

Flanagan, P.W. & Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Can. J. For. Res.* **13**: 795–817.

Fox, R.H., Myers, R.J.K., & Vallis, I. 1990. The nitrogen mineralization rate of legume residues in soil as influenced by their polyphenol, lignin, and nitrogen contents. *Plant Soil* **129**: 251–259.

Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630–2637.

Gershenzon, J. 1984. Changes in the levels of plant secondary metabolites under water and nutrient stress. In: Phytochemical adaptations to stress, B.N. Timmermann, C. Steelink, & F.A. Loewus (eds.). Plenum Press, New York, pp. 273–321.

Gorham, E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climate warming. *Ecol. Appl.* **1**: 182–195.

Griffiths, B.S., Welschen, R., Van Arendonk, J.J.C.M., & Lambers, H. 1992. The effects of nitrogen supply on bacteria and bacterial-feeding fauna in the rhizosphere of different grass species. *Oecologia* **91**: 253–259.

Harris, M.M. & Riha, S.J. 1991. Carbon and nitrogen dynamics in forest floor during short-term laboratory incubations. *Soil Biol. Biochem.* **23**: 1035–1041.

Hättenschwiler, S. & Vitousek, P.M. 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol. Evol.* **15**: 238–243.

Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* **7**: 336–339.

Hobbie, S.E. 1995. Direct and indirect effects of plant species on biogeochemical processes in arctic ecosystems. In: Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences, F.S. Chapin III & C. Körner (eds.). Springer-Verlag, Berlin, pp. 213–224.

Hobbie, S.E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* **66**: 503–522.

Hungate, B.A., Canadell, J.C., & Chapin III, F.S. 1996. Plant species mediate changes in microbial N in response to elevated CO_2. *Ecology* **77**: 2505–2515.

Johnson, L.C. & Damman, A.W.H. 1993. Decay and its regulation in *Sphagnum* peatlands. *Adv. Bryol.* **5**: 249–296.

Kandil, F.E., Grace, M.H., Seigler, D.S., & Cheeseman, J.M. 2004. Polyphenolics in *Rhizophora mangle* L. leaves and their changes during leaf development and senescence. *Trees* **18**: 518–528.

Leyval, C. & Berthelin, J. 1993. Rhizodeposition and net release of soluble organic compounds by pine and beech seedlings inoculated with rhizobacteria and ectomycorrhizal fungi. *Biol. Fertil. Soils* **15**: 259–267.

Middleton, B.A. & McKee, K.L. 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. *J. Ecol.* **89**: 818–828.

Mitchell, M. & Fuller, R. 1988. Models of sulfur dynamics in forest and grassland ecosystems with emphasis on soil processes. *Biogeochemistry* **5**: 133–163.

Nguyen, C. 2003. Rhizodeposition of organic C by plants: Mechanisms and controls. *Agronomie* **23**: 375–396.

Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, E.G., & Canadell, J.G. 2001. Elevated CO_2, litter chemistry, and decomposition: A synthesis. *Oecologia* **127**: 153–165.

Northup, R.R., Yu, Z., Dahlgren, R.A., & Vogt, K.A. 1995. Polyphenol control of nitrogen release from pine litter. *Nature* **377**: 227–229.

Norton, J.M. & Firestone, M.K. 1996. N dynamics in the rhizosphere of *Pinus ponderosa* seedlings. *Soil Biol. Biochem.* **28**: 351–362.

Parmelee, R.W., Ehrenfeld, J.G., & Tate, R.L., III 1993. Effects of pine roots on microorganisms, fauna, and nitrogen availability in two soil horizons of a coniferous forest spodosol. *Biol. Fert. Soils* **15**: 113–119.

Paul, E.A. & Clark, F.E. 1989. Soil microbiology and biochemistry. Academic Press, San Diego.

Pérez-Harguindeguy, N., Diaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido, M., & Castellanos, A. 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant Soil* **218**: 21–30.

Read, D.J. & Perez-Moreno, J. 2003. Mycorrhizas and nutrient cycling in ecosystems – A journey towards relevance? *New Phytol.* **157**: 475–492.

Ruess, R.W., Van Cleve, K., Yarie, J., & Viereck, L.A. 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior taiga forests on the Alaskan interior. *Can. J. For. Res.* **26**: 1326–1336.

Rygiewicz, P.T. & Andersen, C.P. 1994. Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* **369**: 58–60.

Schimel, J.P. & Bennett, J. 2004. Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* **85**: 591–602.

Silver, W.L. & Miya, R.K. 2001. Global patterns in root decomposition: Comparisons of climate and litter quality effects. *Oecologia* **129**: 407–419.

Swift, M.J., Heal, O.W., & Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. Blackwell Scientific Publications, Oxford.

Tate III, R.L. O'Reilly, L., Parmelee, R.W. & Ehrenfeld, J.G. 1991. Nitrogen mineralization: root and microbial interactions in pitch pine microcosms. *Soil Sci. Soc. Am. J.* **55**: 1004–1008.

Van Breemen, N. 1993. Soils as biotic constructs favouring net primary productivity. *Geoderma* **57**: 183–211.

Van Groenigen, K.-J., Six, J., Hungate, B.A., De Graaff, M.-A., Van Breemen, N., & Van Kessel, C. 2006. Element interactions limit soil carbon storage. *Proc. Natl. Acad. Sci. USA* **103**: 6571–6574.

Van Veen, J.A., Merckx, R., & Van de Geijn, S.C. 1989. Plant- and soil related controls of the flow of carbon from roots through the soil microbial biomass. *Plant Soil* **115**: 179–188.

Van Vuuren, Aerts, R., Berendse, F., & De Visser, W. 1992. Nitrogen mineralization in heathland ecosystems dominated by different plant species. *Biogeochemistry* **16**: 151–166.

Verhoeven, J.T.A. & Toth, E. 1995. Decomposition of *Carex* and *Sphagnum* litter in fens: Effect of litter quality and inhibition by living tissue homogenates. *Soil Biol. Biochem.* **27**: 271–275.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I., & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecol. Biogeog.* **14**: 411–421.

Zak, D.R., Blackwood, C.B., & Waldrop, M.P. 2006. A molecular dawn for biogeochemistry. *Trends Ecol. Evol.* **21**: 288–295.

Zhu, W. & Ehrenfeld, J.G. 1996. The effects of mycorrhizal roots on litter decomposition, soil biota, and nutrients in a spodosolic soil. *Plant Soil* **179**: 109–118.